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Novel insights into the marine phase and river fidelity of anadromous twaite shad *Alosa fallax* in the UK and Ireland

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Abstract

1. Most research on anadromous fishes has been invested in their freshwater life-phases, resulting in a relatively sparse understanding of their spatial ecology during marine life-phases. However, understanding the marine dispersal of anadromous fishes is essential to identify threats and to implement conservation measures that fully encompass their lifecycle.
2. The twaite shad *Alosa fallax* is an anadromous fish increasingly imperilled across its range due to pollution, harvesting, and impediments to freshwater migration, but little is known about its distribution and movements during its marine life-phase. Here, the application of acoustic telemetry provided novel insights into the coastal dispersal of twaite shad in the UK and Ireland during 2018–2019, and the freshwater entry of individuals during the 2019 spawning season.
3. Of 73 twaite shad acoustic-tagged during their upstream migration in the River Severn in May 2018, 58 emigrated from the river. Twelve were subsequently detected 200 km to the south-west at the Taw–Torridge Estuary between July 2018 and April 2019, where estuarine movements up to 5.8 km inland occurred in summer, winter, and spring. One was subsequently detected in the Munster Blackwater Estuary (Ireland) and then in the River Severn, indicating a minimum movement distance of 950 km. Thirty-four (59%) of the emigrating individuals from 2018 re-entered fresh water in the rivers Severn (n = 33) and Wye (n = 2) in April and May 2019.
4. These results suggest year-round use of estuarine and nearshore habitats by at least a subset of the twaite shad population during their marine phase, providing evidence of potential range overlap between populations that spawn in different areas in the UK and Ireland, which may be facilitated by substantial dispersal. The results also highlight the potential of telemetry for estimating freshwater and marine mortality, and the benefits of sharing detection data across networks.

KEYWORDS

acoustic telemetry, anadromous fish, data sharing, estuaries, migration, networks

1 | INTRODUCTION

Populations of anadromous fishes are increasingly threatened by anthropogenic disruptions to their lifecycles, occurring in freshwater and marine environments (Limburg & Waldman, 2009). In many anadromous species, the research focus has tended to be on their freshwater life-phase, but marine processes and anthropogenic threats may be a principal driver of population declines in some species and populations (Chaput, 2012). In order to implement conservation measures that fully encompass their lifecycle, a more complete understanding of the marine life-phases of anadromous fish is required (Drenner et al., 2012). Key knowledge gaps relate to their spatial ecology while at sea, including habitat use, dispersal, and mortality rates, as well as population-specific distribution and connectivity (McLean, Hay, & Taylor, 1999). Addressing these knowledge gaps may help to mitigate marine-specific threats, including harvesting and accidental bycatch, and to understand the impacts of human-induced climate change (Dunton et al., 2015).

An anadromous fish that is becoming increasingly imperilled across its range is the twaite shad (*Alosa fallax*), which has a distribution across the north-western Atlantic and Mediterranean. Their riverine migration period lasts for approximately 3 months, with peak river entry periods varying from February in the south of its range to May–June in the north (Aprahamian, Baglinière, et al., 2003). Individuals that have spawned in previous years often represent over 50% of the spawning run (Aprahamian, Aprahamian, Baglinière, Sabatié, & Alexandrino, 2003). After spawning, surviving adults return to the marine environment, and initial seaward migration by the young-of-the-year occurs in summer and autumn (Aprahamian, 1988). Severe declines and extirpations of twaite shad populations in European rivers have been attributed to pollution, overfishing in fresh water, and artificial structures that inhibit their upstream spawning migration (Aprahamian, Baglinière, et al., 2003; Antognazza et al., 2019; de Groot, 1990). Concerns over twaite shad population declines are reflected in conservation legislation, with the species listed in Annexes II and V of the Habitats Directive and Appendix III of the Bern Convention (Aprahamian, Aprahamian, & Knights, 2010). Spawning populations of twaite shad in the UK, where they are subject to additional protection under the Wildlife and Countryside Act, are now limited to four rivers: the Severn, Wye, Usk, and Tywi. Four rivers in Ireland also support spawning populations: the Munster Blackwater and the Barrow–Nore–Suir river system (King & Roche, 2008).

Despite spending the majority of their life at sea, little is known about the movements, feeding areas, distribution, and population overlap of twaite shad in the marine environment (Aprahamian, Aprahamian, et al., 2003), with all previous knowledge obtained indirectly. For example, in the UK and Ireland, spawning populations of twaite shad display genetic isolation by distance (Jolly et al., 2012), suggesting fidelity to natal rivers by returning spawners. Likewise, analyses of landings data have suggested coastal distributions of twaite shad in relatively shallow areas (<50 m depth) that centre around known spawning rivers (Nachón, Mota, Antunes, Servia, & Cobo, 2016; Taverny & Elie, 2001), and modelling of marine catch distribution in the Bay of Biscay and English Channel has suggested a winter migration from coastal to oceanic areas (Trancart, Rochette, Acou, Lasné, & Feunteun, 2014). The impacts of both targeted fisheries and accidental bycatch on twaite shad populations remain poorly understood, and this knowledge gap is compounded by their scarcity, negligible commercial value, and legislative protection in some areas that, in combination, result in a general lack of reporting in fisheries and bycatch statistics (Hillman, 2003).

Acoustic telemetry is a rapidly developing method that is useful for tracking the movements of aquatic species (Hussey et al., 2015). When different groups of researchers share data from networks of acoustic receivers (which detect and record tagged animals in the vicinity) deployed in multiple regions and habitats, the spatial area over which wide-ranging species can be recorded is increased (Taylor, Babcock, Simpfendorfer, & Crook, 2017). The perceived sensitivity of twaite shad to handling and sedation has limited progress in understanding their movements through telemetry (Breine et al., 2017). However, recent refinements have enabled internal transmitter implantation under general anaesthesia in twaite shad, providing a potential opportunity to record individual movements over multiple spawning seasons and during their marine life-phase (Bolland et al., 2019). Correspondingly, the aim of this study was to document the marine detections and subsequent freshwater entry of acoustic-tagged adult twaite shad that emigrated from the River Severn (western England). Using shared detection data from inshore and estuarine receiver arrays in south-west England and south-east Ireland, the objectives were to: (1) identify the location and timing of coastal and estuarine detections of tagged twaite shad that emigrated from the River Severn following spawning; (2) quantify the extent of twaite shad movements into estuaries outside the spawning period; (3) assess the fidelity of repeat-spawning individuals to the River Severn; and (4) provide initial estimates of freshwater, marine, and annual mortality for tagged individuals.

2 | METHODS

In May 2018, 73 upstream-migrating adult twaite shad were surgically tagged with 69 kHz, Vemco V9 programmed acoustic transmitters (www.vemco.com), using the tagging protocol of Bolland et al. (2019), following ethical review and according to UK Home Office project licence PD6C17B56. Twaite shad were captured at two locations (Maisemore Weir, 51.8928, −2.2668, n = 20; Upper Lode Weir, 51.9935, −2.1739 n = 53) using two techniques (angling n = 44, trapping n = 29). Tagging occurred on seven different days between May 9 and May 24, 2018, with between one and 14 fish tagged each day. The mean length ± 95% confidence interval (range) of tagged individuals was 359 ± 7 mm (275–411 mm), and mean weight was 612 ± 40 g (250–950 g) (Supporting Information Table S1). Analysis of spawning-marks on scales on a projecting microscope (×48 magnification) suggested that 43 (58%) of the tagged fish had spawned at least once previously (Supporting Information Table S1).

Acoustic-tagged individuals were tracked in the River Severn using an array of 38 Vemco VR2-W acoustic receivers between early May and mid-June, 2018, as part of a wider programme of work focusing on the spawning migration of twaite shad (Antognazza et al., 2019; Severn Rivers Trust, 2019). Acoustic-tagged twaite shad were classed as having emigrated from the river following their final detection location on the most downstream receiver in the array (51.8347, −2.2901; Figure 1). This receiver was located in the estuary, 8 km downstream of the tidal limit. Fish that failed to emigrate were assumed to have died within the river (e.g. due to predation or failure to recover from spawning activities). At the end of June 2018, the acoustic transmitters switched from a randomized 1 min pulse interval (minimum interval between acoustic pulses 30 s, maximum interval 90 s) to a 10 min pulse interval until April 2019, when they were programmed to switch back to their randomized 1 min pulse interval. The rationale of this programming was to prolong the battery life of the transmitters to approximately 3 years (to enable tracking of three spawning migrations) whilst maintaining the possibility of tagged fish being detected on other receiver arrays during the marine phase of their lifecycle. The shorter delay interval allowed more detailed tracking of individuals entering fresh water during their known breeding season between April and the end of June (Aprahamian, 1988).

To ensure that any subsequent detections of acoustic-tagged twaite shad during the marine phase of their migration were reported, transmitter IDs of emigrating individuals were distributed to researchers at institutions known to be operating acoustic telemetry arrays in western Great Britain and eastern Ireland to track the movements of bass (*Dicentrarchus labrax*), Atlantic salmon (*Salmo salar*), and sea trout (*Salmo trutta*) in multiple coastal and estuarine locations (Table 1; Figure 1). The areas covered by receiver arrays in south-west England were the Taw–Torridge Estuary (*n* = 31 receivers; TT, Figure 1), the Kingsbridge–Salcombe Estuary (*n* = 15; KS), and River Dart estuaries (*n* = 26; RD) (University of Plymouth, 2020). In south-east Ireland, receivers were present in the estuarine reaches of the River Bandon (RB, *n* = 4), Munster Blackwater (MB, *n* = 4), River Barrow (RBA, *n* = 4), River Slaney (RS, *n* = 4), Bannow Bay (BB, *n* = 4), Cullenstown (CU, *n* = 2), and Rogerstown Inlet (RI, *n* = 3) (Marine Institute, 2020). All receivers in these arrays listened at 69 kHz and were thus capable of detecting tagged twaite shad from the Severn. The receivers 1 km outside the estuary mouth at TT (hatched area in Figure 1) were removed between September and November 2018. All other receivers remained active and in place between June 2018 and July 2019.

To identify the rivers entered by returning acoustic-tagged twaite shad in 2019, and thus estimate their rate of return to the River Severn during the spawning period, single receivers were installed in early April 2019 at the tidal limit in the rivers Wye, Usk, and Tywi (Figure 2). These receivers were placed downstream of known twaite shad spawning areas in these rivers (Aprahamian, Lester, & Aprahamian, 1998). In the River Severn, a receiver was placed at the tidal limit (Figure 2). This was in addition to an array of 48 receivers upstream as part of a freshwater investigation (data not reported here). The receivers remained in place until late July 2019, well beyond the conclusion of the known twaite shad spawning season in the region (Aprahamian, Baglinière, et al., 2003).

Freshwater mortality of upstream-migrating acoustic-tagged twaite shad was calculated based on the proportion that did not emigrate from the River Severn. Marine mortality of emigrating individuals was calculated as the proportion of tagged individuals that did not return to fresh water in 2019. Annual mortality of all upstream-migrating twaite shad tagged in 2018 was then calculated by combining freshwater and marine mortality. For the purpose of mortality estimates, emigrating individuals in 2018 that were not detected in fresh water in the rivers Severn, Wye, Usk, or Tywi during the spawning period in 2019 were assumed to have died during their marine phase.

3 | RESULTS

Of the 73 twaite shad acoustically tagged during their upstream spawning migration in the River Severn in May 2018, 58 were detected emigrating from the river; thus, the rate of freshwater

TABLE 1 Acoustic receiver arrays present in estuarine and coastal waters of south-western UK and southern Ireland between May 2018 and July 2019

Country	Estuarine array	Map code	*N* receivers	Deployment period
UK	Taw–Torridge Estuary	TT	31	July–August 2018 until after study period. Note: receivers in hatched box in Figure 1 removed between September and November 2018
	Kingsbridge–Salcombe Estuary	KS	15	July–August 2018 until after study period
	River Dart Estuary	RD	26	Throughout study period
Ireland	River Bandon	RB	4	Throughout study period
	Munster Blackwater	MB	4	Throughout study period
	River Barrow	RBA	4	Throughout study period
	Bannow Bay	BB	4	Throughout study period
	Cullenstown Inlet	CU	2	Throughout study period
	River Slaney	RS	4	Throughout study period
	Rogerstown Inlet	RI	3	Throughout study period

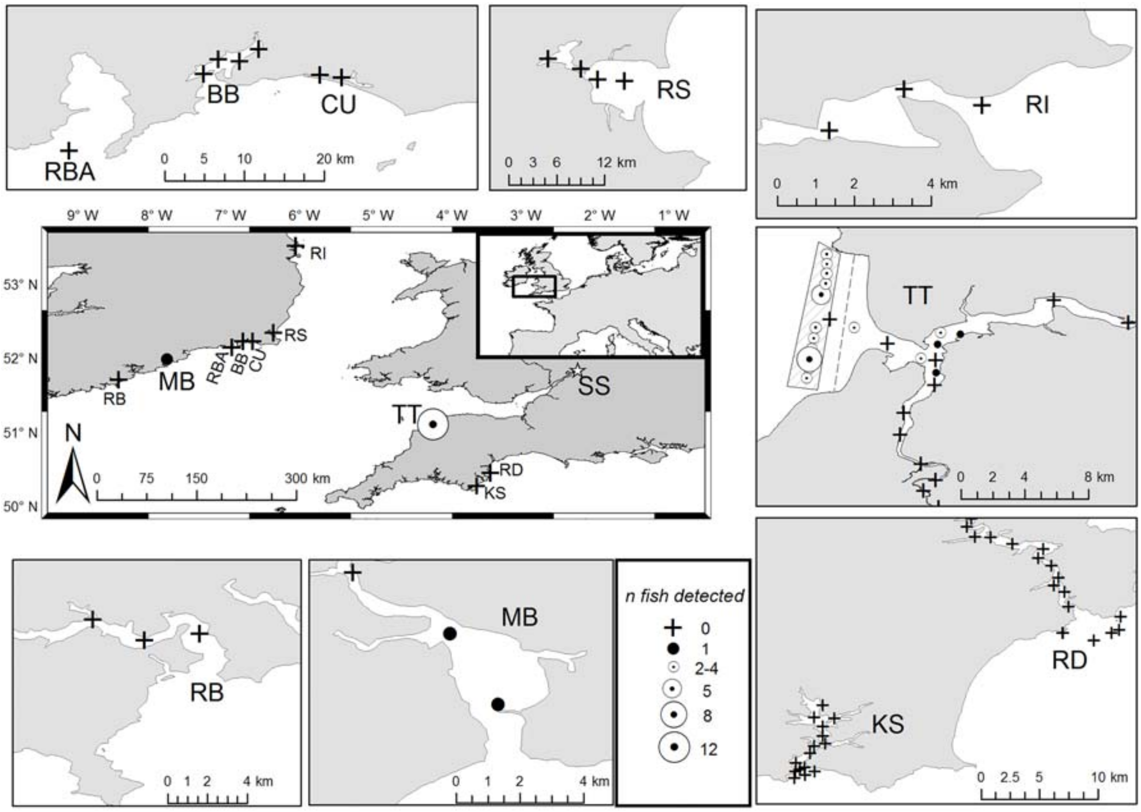

FIGURE 1 Map of the study area used to interpret the marine movements of twaite shad in the western UK and Ireland. SS: final detection location of emigrating post-spawning acoustic tagged fish in the River Severn array in May–June 2018. Circles denote known estuarine arrays (central panel) and specific receivers (outer panels) where shad were detected; + denotes known estuarine arrays and specific receivers where shad were not detected between July 2018 and April 2019. Riverine receivers (n = 3, no detections) in the River Barrow (RBA) not shown

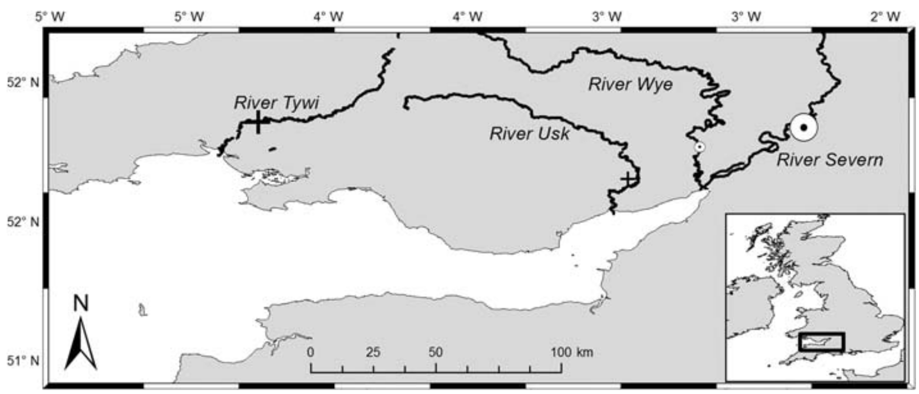

FIGURE 2 Location of freshwater detection of 34 acoustic-tagged twaite shad in April–May 2019 that emigrated from the River Severn post-spawning in 2018. Circles denote the location of receivers at the tidal limit where twaite shad were detected in the River Severn (n = 33) and River Wye (n = 2); **+** denotes the location of receivers in known twaite shad spawning rivers where shad were not detected during the same period. Note: one fish was detected in both the River Wye and River Severn

mortality was 0.21. The median emigration date was June 6 (range May 9 to June 23). Of the 58 emigrating fish, 12 were subsequently detected in north Devon, by the Taw–Torridge Estuary array (Figure 1), representing a minimum movement distance of approximately 200 km from the tidal limit in the River Severn (Figure 1). Detections outside the mouth of the Taw–Torridge Estuary occurred between July and November 2018, but no individual was detected on more than five individual days (Table 2). Also, three of the 12 twaite shad were detected on receivers within the macrotidal Taw–Torridge Estuary (Figure 1), with detections in August 2018, December 2018, and March–April 2019 (Table 2). All detections within the estuary occurred within 2 hr either side of high tide (Bideford Tide Times, www.tidetimes.org).

An individual twaite shad (ID 26250; Table 2) was detected entering the Munster Blackwater Estuary in southern Ireland in December 2018 (Figure 1), 4 months after its last detection in north Devon, with this representing a linear distance of 270 km. Its detection in this estuary coincided with the start of a flooding tide (Youghal Tide Times, www.tidetimes.org), and was subsequently detected returning to the River Severn in late April 2019. Thus, this twaite shad had a minimum movement distance of 950 km during its marine phase between June 2018 and April 2019.

TABLE 2 Summary of acoustic-tagged twaite shad from the River Severn detected in the Taw–Torridge Estuary array. '*n* days detected' refers to the number of distinct days a tagged twaite shad was detected on the array; '*n* journeys into estuary' refers to the number of distinct journeys each individual made from outside the estuary mouth to within the estuary mouth; 'distance into estuary' represents the maximum distance of detection for each individual on estuarine receivers relative to the estuary mouth (cf. Figure 1)

Fish ID	*n* detections	Detection period	*n* days detected	*n* journeys into estuary	Distance into estuary (km)
26317	2	December 2018	1	1	5.8
26330	32	July–August 2018	4	1	5.4
26331	35	March–April 2019	5	2	5.4
26245	1	September 2018	1	n/a	n/a
26248	41	July–August 2018	2	n/a	n/a
26250*	6	August 2018	2	n/a	n/a
26251	2	October 2018	1	n/a	n/a
26258	15	September 2018	3	n/a	n/a
26278	27	August 2018	2	n/a	n/a
26284	12	September 2018	2	n/a	n/a
26,301	2	November 2018	1	n/a	n/a
26309	31	September–November 2018	5	n/a	n/a

*The individual that was subsequently detected in the Munster Blackwater Estuary (Ireland) and the River Severn.

Of the 58 emigrating tagged twaite shad in 2018, 34 (59%) were redetected on receivers in fresh water in April and May 2019 (Figure 2); thus, the rate of marine mortality for the 58 emigrating individuals was 0.41. These returning twaite shad comprised 10 individuals that had been detected on coastal receiver arrays during their marine phase, and 24 not detected since emigrating from the River Severn in 2018. Of the 34 returners, one was detected only in the River Wye (Figure 2), one was detected entering the River Wye before subsequently migrating into the River Severn 1 week later, and 32 were detected only in the River Severn. Combining freshwater and marine mortality, the annual mortality rate for the 73 tagged individuals was 0.53.

4 | DISCUSSION

The detection of 12 twaite shad in coastal environments in the UK and Ireland between July 2018 and April 2019, following their tagging in the River Severn in May 2018, revealed novel insights into the spatial ecology of this threatened species. These initial findings represent the first definitive record of twaite shad dispersal during the marine phase of their lifecycle in the UK and Ireland. In addition, the return of 33 out of 34 individuals to the River Severn in spring 2019 provided new information on the fidelity of twaite shad to the river of their previous spawning, as well as broad estimates of marine mortality.

Evidence regarding the marine distribution of twaite shad elsewhere in Europe has primarily been derived from landings data from coastal and pelagic fisheries which have pointed towards coastal distributions that are centred in shallow marine areas around known spawning rivers (e.g. La Mesa, Annunziatellis, Filidei, & Fortuna, 2015; Nachón et al., 2016; Taverny & Elie, 2001). Whereas others have proposed an offshore migration of twaite shad in northern areas of their range in winter (Trancart et al., 2014), here, the detection of some twaite shad within two estuaries during December suggests that coastal habitats may be used by at least some individuals from the River Severn year-round. At the Taw–Torridge Estuary, during the 5-month period when receivers outside the estuary mouth were in place, individual twaite shad were detected on a maximum of five different days, suggesting a transient use of the immediate coastal area. Recent evidence from otolith microchemistry has suggested a substantial dispersal capacity of twaite shad, with marine-captured individuals shown to originate from rivers up to 600 km away (Nachón et al., 2020). Here, direct evidence is provided to support this, with an estimated minimum 950 km round trip migration made by a returning individual twaite shad to the River Severn. This finding is also consistent with minimum dispersal distances proposed for other *Alosa* fishes (e.g. Dadswell, Melvin, Williams, & Themelis, 1987; Martin et al., 2015). Further telemetry studies may be useful for answering questions on shad marine distribution, potentially, if complemented by otolith microchemistry (Nachón et al., 2020) or genetic studies, to determine their natal origin (Martin et al., 2015).

Here, the detection of a twaite shad in an Irish estuary known to support spawning populations of shad suggests that at least some of the UK and Irish populations share or overlap their ranges. This finding supports recent work indicating that capture location may not be a reliable indicator of origin (Nachón et al., 2020), as well as marine capture data of tagged individuals in other *Alosa* species suggesting that different spawning populations mix at sea (Dadswell et al., 1987; Melvin, Dadswell, & Martin, 1986). Four rivers in south-east Ireland, including the Munster Blackwater, are designated as Special Areas of Conservation under the European Union Habitats Directive because they support spawning populations of twaite shad (King & Roche, 2008). Detection of a tagged individual from the Severn in December suggests these estuaries could provide important habitats for nonspawning individuals belonging to populations from other rivers, and thus their protections could be extended to cover non-spawning twaite shad that spend periods of their winter in these areas.

Of the 34 tagged individuals detected in known UK shad spawning rivers in spring 2019, 33 of 34 (97%) returned to the River Severn. This figure is comparable to a mark–recapture study in American shad *Alosa sapidissima*, where fidelity to a previous spawning river was estimated at 97% (Melvin et al., 1986). Note, however, that in the current study, the possibility of tagged individuals entering rivers without receivers cannot be ruled out. Twaite shad populations in the UK and Ireland display genetic isolation by distance, with spawning populations in the neighbouring rivers Severn and Wye showing a lack of genetic differences, whereas the Tywi, Usk, and Irish populations are genetically distinct from the Severn population (Jolly et al., 2012). This genetic structuring between populations is potentially supported by this study, because no straying of acoustic-tagged individuals into the rivers Usk, Tywi, Munster Blackwater, or Barrow–Nore–Suir was detected during the spawning period, although two were detected in the River Wye (although spawning cannot be confirmed). These observations are in line with those for allis shad *Alosa alosa*, where straying behaviour is more common between neighbouring rivers (Martin et al., 2015). One of the individuals detected in the Wye entered the Severn a week later; it is unclear whether this individual spawned in the Wye or entered as part of an exploratory movement, but its subsequent return to the Severn further supports fidelity to this previous spawning river.

The return of 34 twaite shad to fresh water during the spawning season in 2019 represents the first successful tracking of individuals in this species over multiple spawning seasons. This is a highly encouraging step towards understanding the spatial ecology of repeat spawning migrations, as well as factors affecting annual mortality. Their return provided an initial mortality rate estimate of 0.53 for the original 73 tagged individuals, which is comparable to Aprahamian (1988) (0.53 ± 0.18) and Aprahamian and Lester (2001) (0.47), and slightly lower than Aprahamian et al. (2010) (0.67 ± 0.14), which were estimated from the relative proportion of age classes represented among captured individuals. The marine mortality rate of emigrating individuals between the 2018 and 2019 spawning periods was 0.41, and these figures are broadly comparable to similar studies in repeat spawning sea trout (Aarestrup et al., 2015), although rates of return may be highly population specific (Thorstad et al., 2016). These initial results suggest that further telemetry studies of twaite shad may allow the partitioning of annual mortality into marine and freshwater components, allowing annual variation in mortality rates to be assessed, and individual and environmental factors affecting mortality to be determined (Berg & Jonsson, 1990). Further years of data from returning twaite shad are required to determine whether skipped spawning by adults, as well as the potential effects of tagging and handling on survival, may affect the accuracy of mortality rate estimates (McGarvey, 2009).

The estuary of the River Severn drains into the Bristol Channel, bordered by the coastlines of south Wales and the south-west England peninsula. During the study period the Taw–Torridge Estuary array was the only active acoustic array in this area, covering less than 1% of approximately 600 km of coastline. Considering this sparse spatial coverage, it is perhaps unsurprising that 24 of the 34 tagged twaite shad that re-entered the Severn to spawn in 2019 had not been detected on coastal arrays during the 2018–2019 marine phase of their migration. It was not possible to assess any aspects of their movements between emigrating from the river in 2018 and returning in 2019, including whether they remained coastally distributed within the Severn Estuary/Bristol Channel, used other river estuaries, or indeed were entirely oceanic during their marine phase. Likewise, individuals detected in the Taw–Torridge were recorded on a maximum of five different days, representing only a small fraction of their time in the marine environment. Dedicated acoustic telemetry studies on the marine phase of twaite shad in this region would benefit from a greater spatial coverage of acoustic receivers, especially if used in conjunction with reduced tag pulse interval to increase the probability of detection on coastal arrays. These actions should provide greater resolution on the marine movements of twaite shad, which could then be used to inform conservation strategies that aim to protect the species throughout its lifecycle.

The results presented here highlight the general paucity of knowledge regarding the movements of twaite shad during their marine phase, and the potential benefits of addressing this knowledge gap for shad conservation. For example, the supposed overlap in non-spawning range and potentially extensive migration of twaite shad suggests a need for cooperative management in the marine environment between the UK and Ireland. This includes more thorough recording of accidental commercial bycatch and recreational capture, beyond the current level of anecdotal data (Hillman, 2003), and bycatch statistics which often do not distinguish between twaite and allis shad (Centre for Environment, Fisheries and Aquaculture Science, unpublished data). Further, the apparent fidelity shown by twaite shad to previous spawning rivers highlights the potential local benefits of population-specific management actions aimed at increasing survival of these returning adults, such as strictly minimizing estuarine and early marine mortality, and river restoration to increase freshwater survival (Waldman, Wilson, Mather, & Snyder, 2016). Finally, the results here would not have been gained without the sharing of telemetry data between three organizations across two European countries. Abecasis et al. (2018) noted that though the rate of publication of acoustic telemetry papers in Europe increased sevenfold between 2007 and 2017, only one study (Huisman et al., 2016) featured an acoustic array that spanned more than one country. This study highlights the potential benefits of implementing a coordinated acoustic tracking network in Europe (and beyond) (Reubens et al., 2019) for providing vital information on the movements of this and other poorly understood migratory species.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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